

## Continuous long-term monitoring of daily foraging patterns in three species of lappet moth caterpillars (Lasiocampidae)

CLAUDIA RUF\*, BERND KORNMAIER & KONRAD FIEDLER

Department of Animal Ecology I, University of Bayreuth, D-95440 Bayreuth, Germany

\* corresponding author: Claudia Ruf, e-mail: Claudia.Ruf@uni-bayreuth.de

**Summary.** Activity patterns of caterpillars of three species of Lasiocampidae were long-time monitored by electronic data acquisition. We used these data to test the hypothesis that the coloration of a caterpillar corresponds to its activity patterns. Caterpillars with warning colours (usually supposed to be chemically or physically well-defended) should forage conspicuously throughout the day whereas cryptic caterpillars (supposed to be 'palatable') should have behavioural mechanisms for reducing exposure to natural enemies (hiding, nocturnal feeding). In terms of predator avoidance and thermoregulation social caterpillars should be strongly synchronized when foraging. Social caterpillars of *Eriogaster lanestris* (Linnaeus, 1758) were strongly synchronized and fed day and night, but synchronicity was low during moulting time and at the end of the last instar. Caterpillars of *Macrothylacia rubi* (Linnaeus, 1758) despite their aposematic colour and urticating hairs proved to be strictly nocturnal while larvae of *Gastropacha populifolia* ([Denis & Schiffermüller], 1775), which are cryptically coloured, were active by day and night. Comparisons with other Lasiocampidae further corroborate the suggestion that there is no correspondence between colour and activity patterns. As a priori judgements of aposematism are doubtful, if not tested explicitly, abiotic factors and life history traits seem to be of greater importance in shaping activity patterns of these caterpillars.

**Zusammenfassung.** Die Aktivitätsmuster von Raupen dreier Lasiocampiden-Arten wurden mittels elektronischer Datenerfassung langfristig überwacht. Mit den so gewonnenen Daten wurde die Hypothese überprüft, daß die Färbung der Raupe mit ihrem Aktivitätsmuster in Zusammenhang steht. Raupen mit Warntracht, von denen in der Regel angenommen wird, daß sie chemisch oder physikalisch wehrhaft sind, sollten tagsüber wie nachts auffällig sein und fressen. Kryptisch gefärbte Raupen dagegen, von denen vermutet werden kann, daß sie 'freßbar' sind, sollten Verhaltensmechanismen besitzen, die ihren Kontakt zu natürlichen Feinden vermindern sollten (Verstecken, nächtliche Futtaufnahme). Soziale Raupen wiederum sollten ihre Aktivität streng synchronisieren, um ihre Auffälligkeit gegenüber Prädatoren so gering wie möglich zu halten und thermoregulatorische Vorteile des Sozialverhaltens zu maximieren. Die sozialen Raupen von *Eriogaster lanestris* (Linnaeus, 1758) erwiesen sich hinsichtlich ihres Fouragierverhaltens als stark synchronisiert und fraßen tagsüber und nachts. Während der Häutungsphasen war die Synchronität allerdings wenig ausgeprägt und schwächte sich zum Ende des letzten Larvenstadiums immer mehr ab. Trotz ihrer Warntracht und ihrer Brennhaare erwiesen sich die Raupen von *Macrothylacia rubi* (Linnaeus, 1758) als strikt nachtaktiv, während Raupen von *Gastropacha populifolia* ([Denis & Schiffermüller], 1775), die kryptisch gefärbt sind, bei Tag und Nacht aktiv waren. Der Vergleich mit anderen Lasiocampidenarten unterstützt die Vermutung, daß es keinen zwingenden Zusammenhang zwischen der Färbung und dem Aktivitätsmuster gibt. Da die Beurteilung von Aposematismus a priori stets zweifelhaft ist, sofern dies nicht explizit geprüft wurde, scheinen abiotische wie biotische Faktoren (z.B. Life-history-Eigenschaften) einen größeren Einfluß auf das Aktivitätsmuster von Lasiocampiden-Raupen zu haben.

**Résumé.** Les modèles d'activité des chenilles de trois espèces de Lasiocampidae ont été recensées sur une longue période au moyen d'acquisition de données électronique. Nous avons utilisé de ces données afin de tester l'hypothèse selon laquelle la coloration d'une chenille correspond à ses modèles d'activité. Des chenilles à couleurs alarmantes (généralement supposées comme bénéficiant d'une bonne protection chimique ou physique) devraient se nourrir la journée entière tout en étant bien visibles, tandis que les chenilles cryptiques (supposées "commestibles") devraient montrer des mécanismes de comportement de nature à réduire leur exposition à des ennemis naturels (mœurs cachées, nutrition exclusivement nocturne). En termes d'évitement de prédateurs et de thermorégulation, des chenilles sociales devraient être fortement synchronisées quant à leurs périodes de nutrition. Les chenilles sociales de l'espèce *Eriogaster lanestris* (Linnaeus, 1758) étaient fortement synchronisées et se nourrissaient de jour comme de nuit, mais la synchronisation était faible lors des mues et à la fin du dernier état larvaire. Les chenilles de *Macrothylacia rubi* (Linnaeus, 1758), malgré leur coloration aposématique et leurs poils urticants, se sont avérées strictement nocturnes, alors que les chenilles de *Gastropacha populifolia* ([Denis & Schiffermüller], 1775), qui sont cryptiques, étaient actives tant de nuit que de jour. Des comparaisons avec d'autres Lasiocampidae corroborent également la suggestion comme quoi il n'y a pas de

correspondence entre la couleur et les modèles d'activité. Les jugements a priori quant à l'aposématisme étant douteux quand ils ne sont pas testés explicitement, il semble que des facteurs abiotiques et des traits biologiques soient de plus grande importance lors de la détermination des modèles d'activité de ces chenilles.

Key words. Lepidoptera, Lasiocampidae, caterpillars, automated monitoring, activity patterns, coloration, *Eriogaster*, *Macrothylacia*, *Gastropacha*.

## Introduction

The major task of lepidopteran larvae is to feed and accumulate resources that will become the main and sometimes even the sole supply of energy for activity and reproduction in later life. Frequently the amount of assimilated food which is directly reflected in body mass of the imago correlates with fitness (Honěk 1993). Accordingly one would predict that caterpillars should feed both day and night, if only limited by abiotic conditions, especially temperature which determines physiology of ingestion and digestion of food. However, caterpillars are slowly moving insects which are the target of a huge number of predators and parasitoids. Caterpillars are therefore forced to evolve mechanisms to minimize exposure to natural enemies while optimizing food intake. This trade-off affects foraging behaviour and activity patterns, preventing caterpillars from unlimited foraging (see Stamp & Casey 1993 and references therein).

Heinrich (1979, 1993) suggested that activity patterns of caterpillars are influenced by their colour and morphological defensive structures. Aposematic caterpillars with spines and chemical defence are supposed to be unpalatable allowing those species to feed in an exposed position in the vegetation by day and night. In contrast, cryptically coloured caterpillars which are expected to lack a chemical or morphological defence and are therefore supposed to be palatable should hide and evolve a foraging schedule that minimizes their encounters with visually hunting predators.

The biology of caterpillars is comparatively poorly studied because they are not as apparent as the imagoes. Hence, apart from a number of pest species, there is only little information on most behavioural patterns. Most information on activity patterns of caterpillars so far available is based on intermittent visual observation and only provides an incomplete picture.

Monitoring caterpillars with customary techniques (e.g. videotaping) is expensive and time-consuming but discloses lots of behavioural details. However, caterpillars do not show very diverse behavioural patterns: they mainly switch between phases of rest and foraging, only interrupted during moults when resting time is prolonged. If one is primarily interested in the activity patterns simple and inexpensive techniques are far more suitable for monitoring activities.

We here introduce an inexpensive, yet precise method of recording caterpillar activity by continuous electronic long-time monitoring of the foraging schedule of three different Lepidopteran species under laboratory conditions. Data are directly recorded by a computer which makes exact counting possible and which is advantageous over techniques like event recorders or data logger (e.g. Fitzgerald *et al.* 1988; Lance *et al.* 1986; Fitzgerald 1980) previously used to measure activity patterns.

The three species under consideration all belong to the moth family Lasiocampidae, one species with social caterpillars (*Eriogaster lanestris* (Linnaeus, 1758)) and two solitary species which differ in coloration (aposematic: *Macrothylacia rubi* (Linnaeus, 1758) and plant-mimetic: *Gastropacha populifolia* ([Denis & Schiffermüller], 1775).

According to Heinrich's hypothesis that activity patterns can be predicted from the caterpillar's external appearance we expected that the solitary aposematic species should be active by day and night, while the solitary cryptic species should hide at the bark and restrict foraging to the night. In the case of social caterpillars one would further predict high within-colony synchronicity of individuals to minimize time of consciousness to predators, at least for activity during the day. Moreover, collective thermoregulation also requires well synchronized activities.

## Methods

**Animals.** – Whole colonies of *E. lanestris* were collected in the field (near Würzburg, Germany) and transferred to an environmental cabinet with a 14:10 L:D light regime. Temperature changed between 15°C at night and 22°C during the days. For one colony temperature was changed manually and varied from 18°C (night) and 25°C (day). Caterpillars live communally in a silken tent which is used as a home base and does not include food resources (Ebert 1994). Therefore caterpillars are forced to leave the tent for every foraging bout (so called 'central place foraging', Fitzgerald & Peterson 1988). Caterpillars are totally black during the first three instars, whereas they develop tufts of flaming red hair in the fourth and fifth instar which are urticating (Pro Natura 2000).

Caterpillars of the solitary species *Macrothylacia rubi* (from Bayreuth, Germany) and *Gastropacha populifolia* (from Gmunden at the Traunsee, Austria) were reared ex ovo by collecting a gravid female or were obtained by a breeder respectively. Both species were held in an environmental cabinet with a 18:6 h (L:D) light regime and 25/18°C temperature (day/night). Temperature was decreased one hour before dusk, and increased with the onset of dawn. This was aimed at experimentally decoupling the potential stimuli that trigger nocturnal activity (drop in temperature, or light intensity).

Caterpillars of *Macrothylacia rubi* are black or dark brown with bright yellow intersegmental membranes during the first four instars. In the last instar they are covered with dense long and short urticating hair (Pro Natura 2000).

Caterpillars of *Gastropacha populifolia* are greyish brown. Dorsal hair is reduced and the shape of the larva is dissolved by lateral lappets which are pressed to the bark (twig mimic). There are two transversal bands of black lancet shaped setae with a tinge of blue in the second and third thoracic segment which are invaginated while at rest and can be everted when the caterpillar is disturbed.

**Measuring activity patterns.** – Quantifying activity patterns was realized by using infrared light barriers with IR diodes (type LD 271) as emitters and IR photo transistors with daylight filter (type SFH 309 F) as receptors. Signals of the light barriers were taken up by a AD/DA card (Decision Computer International Taiwan). Signals were smoothed by an expressly written software which was also used to set a

trigger threshold to eliminate interference and to set a dead time. The counter was read once every minute and the count as well as the time of day were written into a file. Temperature in the environmental cabinet was also measured electronically once a minute with the help of thermal sensors (thermistors type SEMI 833 ET) which were calibrated by an additional software.

Light barriers were co-ordinated differently according to the requirements of the three species investigated (see below).

*Eriogaster lanestris*: Central-place foraging social caterpillars can be monitored easily by forcing the caterpillars of a colony to pass a wooden rod linking their tent with a bunch of blackthorn twigs, *Prunus spinosa*, kept in water. Light barriers were attached beside this rod thus counting all caterpillars passing by during their way to their host plant and back (Fig. 1A). Direct observation showed that caterpillars always walk on the upper side of the rods unless too many caterpillars pass by during the same time. Although single caterpillars were not counted correctly there was no significant difference between direct observational counts and computer based counts ( $t(18df, N=20) = 0.97, p > 0.05$ ).

Seven colonies were monitored over a period of several weeks starting during their 3<sup>rd</sup> instar.

To assess synchronicity of caterpillars of *E. lanestris* an index was calculated by dividing the cumulated number of signals of a whole day by the cumulated number of minutes with at least one signal being recorded. Thus the index is a measurement for the density of occurring signals. High signal density indicates strong group cohesion and high synchronicity.

*Macrothylacia rubi*: Observations revealed that caterpillars always left their host plant after feeding and tried to hide in the rearing box. To monitor activity patterns we prepared a plastic box as represented in Fig. 1B: A watered twig of raspberry (*Rubus*

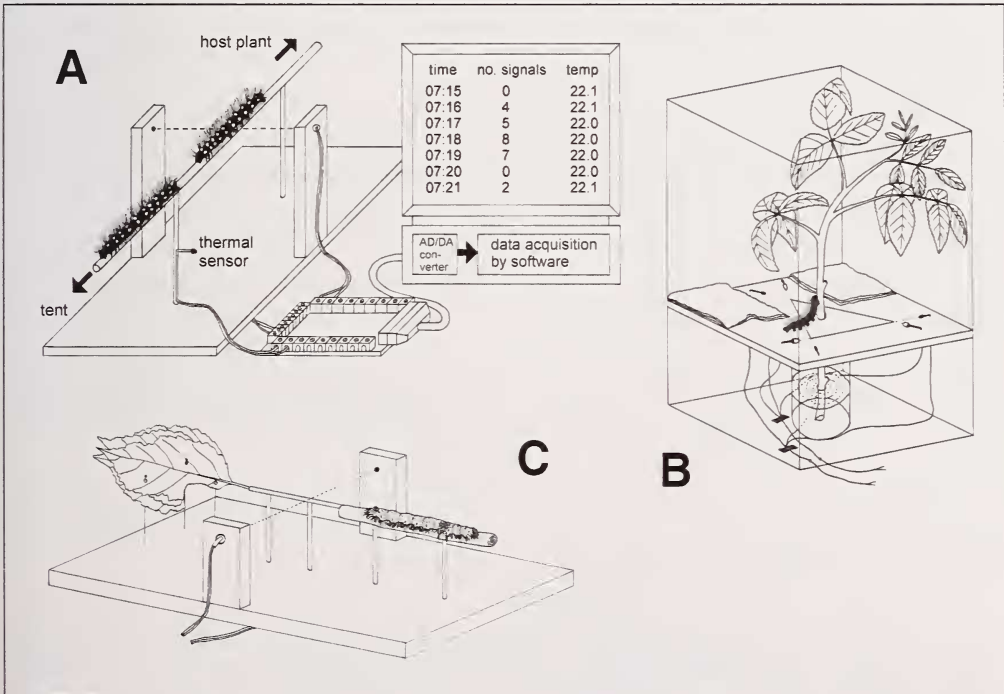
**Tab. 1.** Comparison of activity patterns of different caterpillars within the Lasiocampidae. Colours are judged as aposematic or cryptic from a human perspective. \*: species multivoltine under laboratory conditions (C. Ruf, pers. obs.).

Species	Color	Defense	Voltinism under field conditions	Activity pattern	Place of observation	Reference
<b>Social caterpillars</b>						
<i>Eriogaster lanestris</i> (Linnaeus, 1758)	aposematic	strongly urticating hairs	strictly univoltine (early spring caterp.)	day and night	laboratory, field	this study
<i>Malacosoma americanum</i> (Fabricius, 1793)	aposematic	(weakly) urticating hairs	strictly univoltine (early spring caterp.)	day and night	laboratory, field	Fitzgerald <i>et al.</i> , 1988
<i>Gloveria</i> sp. Packard, 1872	aposematic	urticating hairs	univoltine	nocturnal	laboratory, field	Fitzgerald & Underwood, 1998
<i>Eutachyptera psidii</i> (Sallé, 1857)	aposematic	urticating hairs	univoltine (?)	nocturnal	field	Comstock, 1957
<b>Solitary caterpillars</b>						
<i>Macrothylacia rubi</i> (Linnaeus, 1758)	aposematic	strongly urticating hairs	strictly univoltine	nocturnal	laboratory	this study
<i>Euthrix potatoria</i> (Linnaeus, 1758)	aposematic	urticating hairs	univoltine	nocturnal	field	Pro Natura, 2000
<i>Cosmotriche lobulina</i> ([Denis & Schiffermüller], 1775)	aposematic	?	univoltine *	day and night	laboratory	C. Ruf, pers. obs.
<i>Poecillocampa populi</i> (Linnaeus, 1758)	cryptic	none	univoltine	nocturnal	field	Pro Natura, 2000
<i>Dendrolimus pini</i> (Linnaeus, 1758)	cryptic	hairs in transversal bands?	univoltine / bivoltine *	nocturnal	laboratory, field	Herrebout <i>et al.</i> , 1963, C. Ruf, pers. obs.
<i>Sirebote panda</i> Hübner, 1820	cryptic	hairs in transversal bands?	multivoltine	nocturnal	laboratory	Gómez de Aizpúrua, 1988, C. Ruf, pers. obs.
<i>Gastropacha populifolia</i> ([Denis & Schiffermüller], 1775)	cryptic	hairs in transversal bands?	bivoltine *	day and night	laboratory	this study

*idaeus*) was surrounded by a triangle of light barriers. In the corner of the box folded tissue paper was offered to the caterpillar as shelter. Every time a caterpillar wanted to feed or leave the plant it had to pass the light barriers. Four individual caterpillars were monitored in this way for more than a month each.

*Gastropacha populifolia*: Observations showed that caterpillars rest on thick twigs not far away from their feeding sites. Monitoring was realized by offering a natural poplar twig for resting which was joined with some fresh poplar leaves (*Populus* spp.) by a small wooden rod (Fig. 1B). The light barriers were fixed left and right of the small rod. After feeding caterpillars turned round and walked up to the end of the twig, where they rested until the onset of the next feeding period. During numerous hours of observation caterpillars never chose the underside of the twig neither to walk nor to rest. Thus we can almost rule out the possibility that foraging periods were overlooked when caterpillars avoided the light barriers. The whole construction was placed in a big plastic box lined with wet tissue paper to maintain high humidity. This was necessary to prevent the poplar leaves from quick withering. Ten individual caterpillars were monitored for 2 to 4 weeks each. Caterpillars were kept isolated until eclosion of the moths to determine the sex of the animal.

Obtained data were analyzed statistically using standard procedures with the software package STATISTICA '99.



**Fig. 1.** Methods for monitoring activity patterns of three species of lepidopteran larvae. – **A.** *Eriogaster lanestris*. – **B.** *Macrothylacia rubi* (size of plastic box: 30 × 20 × 20cm). – **C.** *Gastropacha populifolia* (size of PVC board: 20 × 12cm). Data processing was the same for all experimental designs as shown in Figure A.

## Results

*Eriogaster lanestris*. – Monitoring data of all colonies were uniform. During the course of a day there was a sequence of strongly synchronized foraging bouts, as opposed to communal resting times when only few single caterpillars were active (Fig. 2A).

At the onset of an activity period caterpillars started walking around the tent and showed marked spinning behaviour (at least in the first four instars). Caterpillars then suddenly started leaving the tent *en masse*. After feeding caterpillars directly returned to the tent and stayed inactive until the onset of the next activity period. With the exception of the early morning when caterpillars ‘basked’ on the tent before their first daytime foraging bout, they always entered the tent after foraging periods.

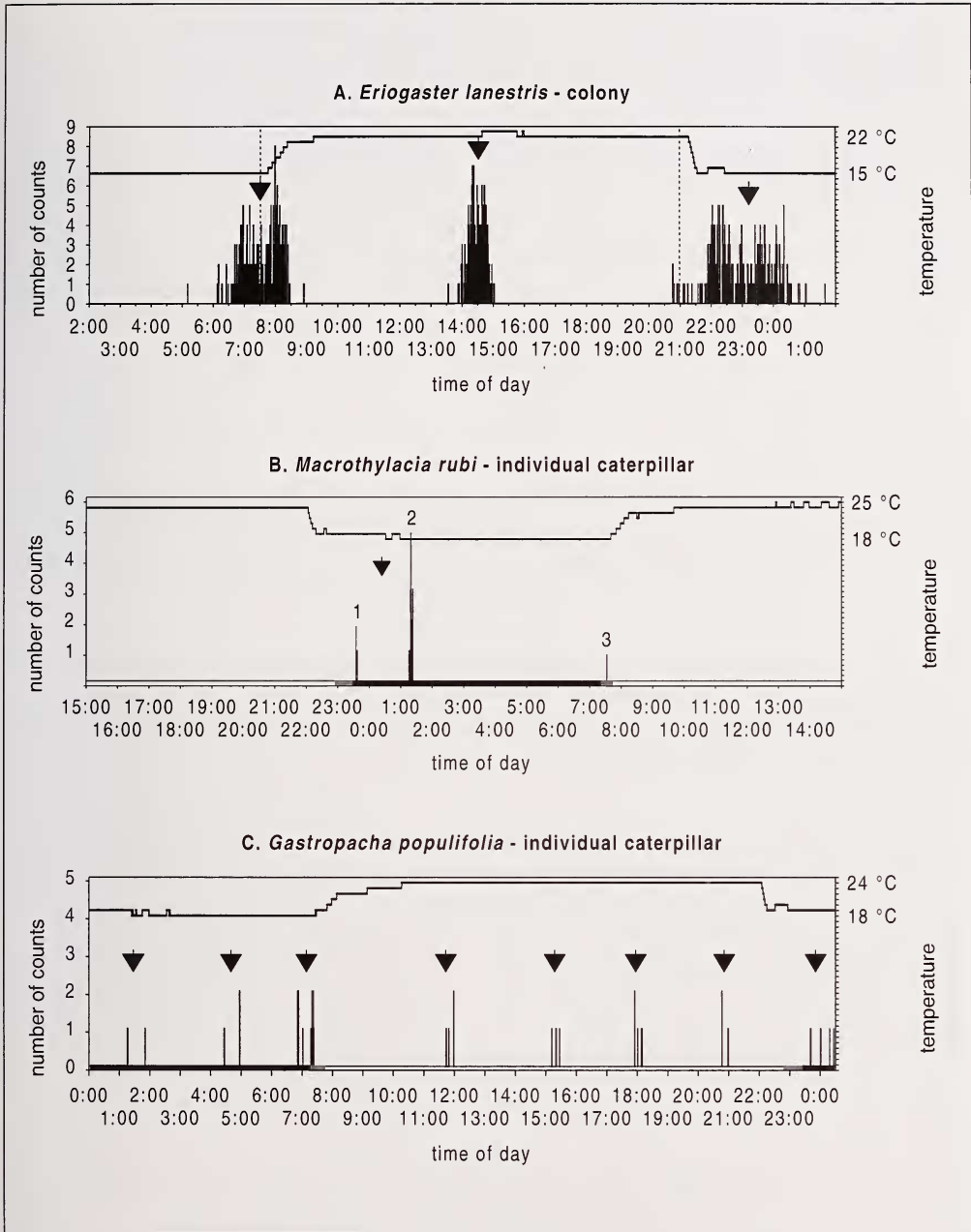
Foraging bouts took place by day and night. When temperature changed between 15°C (night) and 22°C (day) colonies usually undertook three foraging periods per day but sometimes one or two additional foraging bouts occurred. The colony kept at higher temperatures left the tent 4 to 6 times a day, indicating that foraging is opportunistic and does not follow a fixed pattern. This assumption is corroborated when comparing intervals between foraging bouts. These intervals coincide with the time for digestion and depended on predominant temperatures, being shorter when temperatures were higher (Kruskal Wallis ANOVA:  $H(2df, N=30) = 13.74, p < 0.01$ ). Digestion periods at high temperatures (25°C) differed significantly from those at cold temperatures (15 °C) and those at transient temperature. Duration of foraging periods itself also proved to be temperature dependent (Comparison of 25°C / 18°C: Mann-Whitney U-test:  $Z(N=31) = -4.7, p < 0.0001$ ).

Synchronicity was not constant over time. In all colonies synchronicity broke down during the moulting periods and was less pronounced in the last instar (Fig. 3). When the first caterpillars start leaving the tent for pupation the colony breaks up into subgroups, which results in only indistinctly separable activity and resting periods.

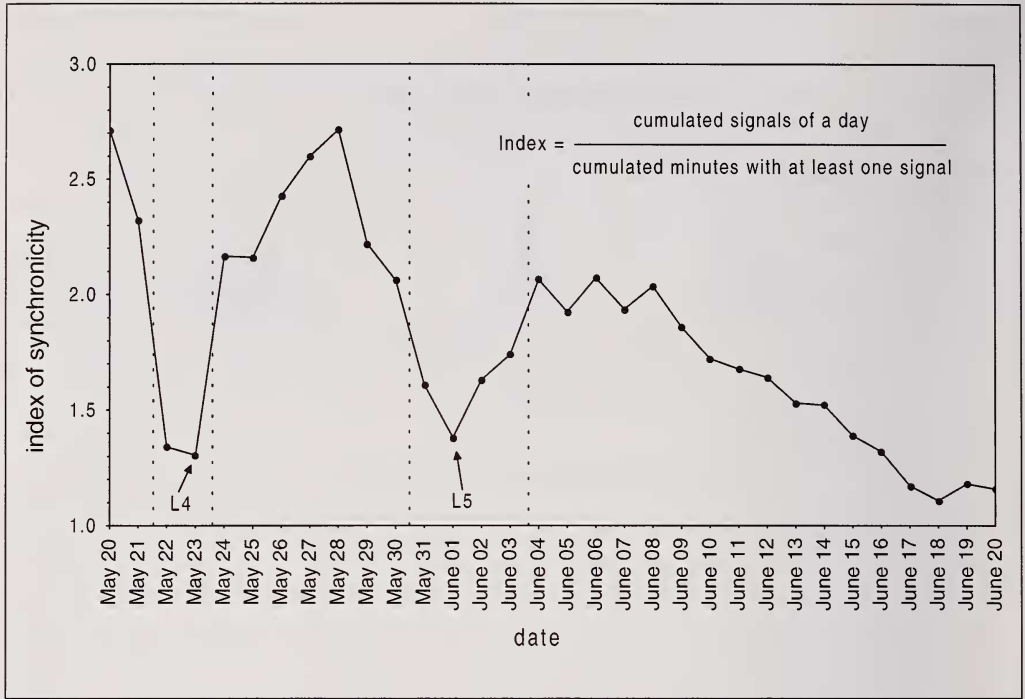
*Macrothylacia rubi*. – Activity of caterpillars of *M. rubi* was completely restricted to nocturnal foraging. Caterpillars first left their hiding place with the onset of total darkness (Fig. 2B, 1) and fed for about two hours ( $114 \pm 42\text{min}$  (mean  $\pm$  SD),  $N = 89$  activity periods, pooled data of all caterpillars). Caterpillars then left the plant (Fig. 2B, 2), sometimes by dropping off, thus getting round the light barrier without passing through the beam. No later than at onset of dusk caterpillars looked for a hiding place where they rested during the whole day (Fig. 2B, 3).

Although high temperatures in the laboratory are favourable to ecdysis, moulting time proved to be extremely long in *M. rubi*. Caterpillars stayed in their hiding place for four days before moulting and again one day afterwards (Fig. 4).

*Gastropacha populifolia*. – Caterpillars of *G. populifolia* proved to be highly active by day and night, showing a steady sequence of feeding and resting irrespective of temperature or light regime (Fig. 2C). The number of foraging periods varied between individuals and larval instars, ranging from 3 to 10 per day, but no consistent pattern could be detected. Temperature did not influence the duration of intervals between the foraging periods (time for digestion) significantly (one-way ANOVA design with repeated measurements ( $N=9$  for all categories,  $F_{1,8} = 1.70, p=0.23$ ).



**Fig. 2.** Comparison of daily activity patterns in caterpillars of three different lasiocampid species. Arrows indicate one foraging period. Changes of light regime are indicated by dashed vertical lines (A) or a black and white baseline (B, C). – **A.** *Eriogaster lanestris*: social, active by day and night. – **B.** *Macrothylacia rubi*, solitary, ‘aposematic’, strictly nocturnal. – **C.** *Gastropacha populifolia*: solitary, active by day and night, ‘cryptic’. Note that time axes are different in all graphs for better visibility of all activity periods.



**Fig. 3.** Change of synchronicity in a colony of *E. lanestris* from the late 3rd instar until the members of the colony disperse before pupation. Areas between vertical lines indicate moulting periods, arrows show the date when the first caterpillar of the next instar was detected.

Duration of foraging period depended on temperature, being twice as long during the night (daytime:  $22 \pm 12$ min (N=283; T=25°C); night:  $40 \pm 19$ min (N=274; T=18°C), means  $\pm$  SD, pooled data). Activity periods of male caterpillars tended to be shorter on average than those of females. Nevertheless, only the effect of temperature was statistically significant (two-way ANOVA design with repeated measurements (N=15 for all categories, effect of temperature:  $F_{1,14} = 28.5$ ,  $p < 0.001$ , Effect of sex:  $F_{1,14} = 3.1$ ,  $p = 0.10$ ). Moulting time is characterized by an interruption of feeding for about 2.5 days.

## Discussion

The method presented here differs from those published elsewhere (Fitzgerald *et al.* 1988; Lance *et al.* 1986; Fitzgerald 1980) with respect to comfortable data management. Data are already analyzed in part because the software does not only provide records of the darkening of the light barrier but real counting events. By saving data in a common file format, they can be processed quickly. However, the method implies that caterpillars always leave their feeding place and do not rest directly in the vegetation after feeding. Thus it is, for example, inapplicable to species living and feeding on herbaceous plants.



Continuous long-term monitoring of caterpillar activity by electronic means has at least three great advantages. First, it allows to study cyclic activity patterns over substantial periods of time, which would be impossible through direct observation. Second, disturbance of animals through the observer can be minimized, since only once a day the animals need to be disturbed (when exchanging food). Third, 'rare' behaviours which occur during short periods, such as foraging movements in *M. rubi*, are reliably recorded, but could easily be missed under direct observation.

Our results indicate different strategies in foraging behaviour between species which do not fit the predictions made: Despite its 'aposematic' colour and defence through urticating hairs *M. rubi* surprisingly restricts foraging to the night whereas *G. populifolia* is active throughout the day and feeds whenever digestion has been completed.

At least for *G. populifolia* these results are inconsistent with qualitative observations made in rearing containers where caterpillars were reported to be 'mainly active by night' (Pro Natura 2000). Caterpillars of *M. rubi* can often be observed in late summer during sunny days (e.g. Ebert 1994). However this behaviour most likely serves thermoregulation (sun-basking) rather than the intake of new food. Since in our experimental conditions radiation from artificial light sources was too low to allow for basking behaviour, it is not surprising that no such behaviour was recorded.

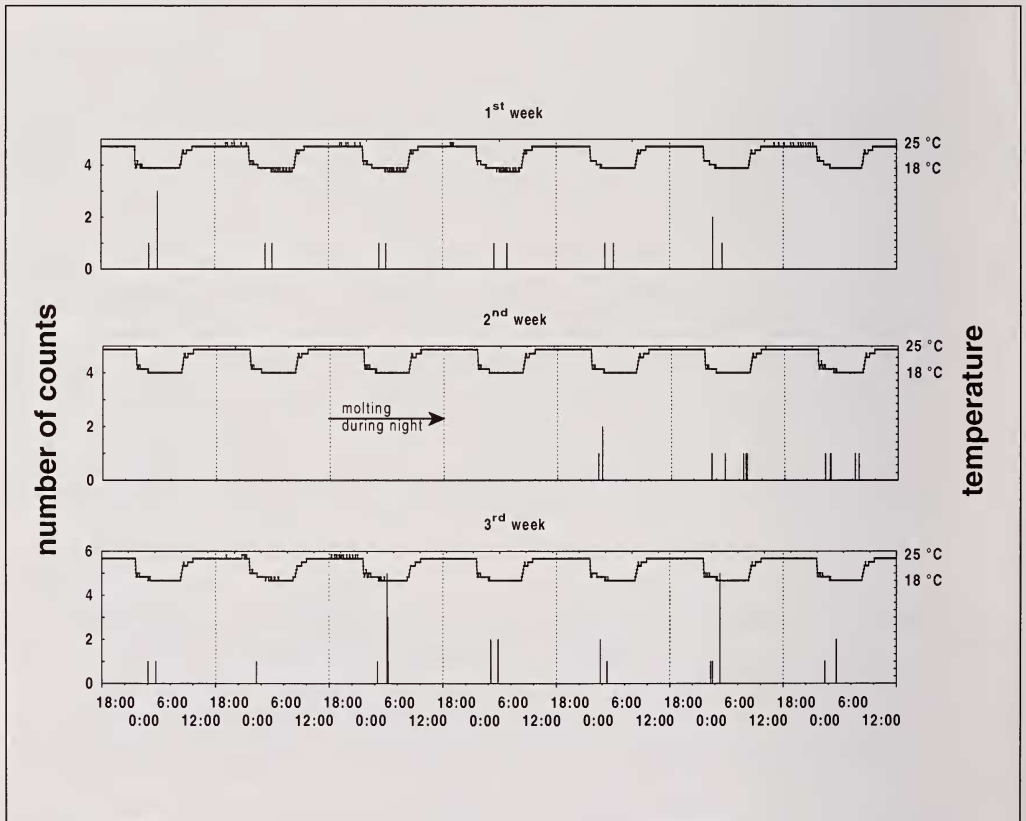
Social larvae of *E. lanestris* foraged in a highly synchronized manner as could be expected in terms of predator avoidance. In our laboratory studies caterpillars were active by day and night. Again, these results are not fully consistent with qualitative observations because published reports on activity patterns in this species vary a lot, ranging from 'active by day and night' (Balfour-Browne 1933) to 'only active by day' or 'only active by night' (Carlberg 1980 and references therein). These inconsistencies in published literature again point to the promising opportunities offered by automatic supervision of caterpillar activity patterns. Evidently, conclusions drawn from intermittent observations and not accounting for environmental conditions may be misleading.

Since our studies took place under standardized laboratory conditions with caterpillars reared in the laboratory which never had experienced any contact to natural enemies, one should expect these larvae to exhibit behaviours which are not modified by biotic or extreme abiotic factors. Obviously selective pressures other than those to enhance food intake or to hide from predators must have played a significant role in shaping feeding behaviour, resulting in the strong interspecific (and probably genetically determined) differences. Abiotic factors may affect foraging behaviour of caterpillars in several ways. High temperatures during daylight may restrict foraging to the night in desert species (Casey 1976), whereas deep temperatures in the night restrict foraging to warm days in arctic caterpillars (Kukal 1993). Anyhow, most caterpillars feed day and night when temperatures in the laboratory are moderate (Casey 1976), indicating that strictly nocturnal or diurnal activity as displayed under natural conditions may often not be fixed genetically.

In our study temperature was always moderate and would have allowed, for physiological reasons, for uninterrupted food intake and processing. Since food was definitely digested in a few hours after feeding caterpillars should therefore not give up

many hours of potential feeding and growing time in daylight, to feed only at lower temperatures in the night. Basically, feeding only at night is costly in terms of time, particularly in north-temperate regions where night-time is short. Nevertheless, caterpillars of *M. rubi* exhibit a strictly nocturnal foraging pattern. Thus, the pattern of foraging only once a day appears as an innate and presumably adaptive behaviour rather than a temporary, environmentally constrained behaviour imposed on a caterpillar by the climatic conditions.

The most common explanation for nocturnal activity is related to the avoidance of visually hunting predators, such as birds. It is generally assumed that most mortality in caterpillars is caused by avian predators (Heinrich & Collins 1983), which is supported by the fact that caterpillars are frequently the main diet for young birds (Nour *et al.* 1998; Seki & Takano 1998). Additionally many caterpillars seem to be perfectly camouflaged by colour or by dissolving the shape of its body which is only useful against predators with a highly evolved visual performance.



**Fig. 4.** Activity pattern of one individual caterpillar of *Macrothylacia rubi* over the course of three weeks. Molting time is extremely long in this species and caterpillars may abandon feeding for five consecutive days. The space between two vertical dashed lines refers to a period of 24 hours.

However, studies on the effectiveness of cryptic coloration of caterpillars in evading predators are incomplete. Nonetheless, there is considerable indirect evidence that cryptic coloration and behaviour reflect the need to avoid predators and thus play an important part in the foraging pattern of insect herbivores (Stamp & Wilkens 1993).

The main problem in judging a caterpillar either to be aposematic or cryptically coloured is caused by the human observer. Scoring a prey as 'cryptic' or 'apparent' depends on the distance between predator and prey and on the discriminatory abilities of the predator (and not that of a human observer) (Endler 1978, 1990). This means that only the predator's perception is relevant for the quality of a caterpillar's crypsis. Studies which include the ultraviolet spectrum indicate that most of the 'cryptically coloured' species investigated were really cryptic to UV sensitive birds but some did not match the background and must be clearly visible to birds (Church *et al.* 1997). Similar qualifications apply if the aposematic nature of a colour pattern is inferred solely on the basis of human perception.

Hairy caterpillars can cause severe contact dermatitis in humans (also called erucism) (Kawamoto & Kumada 1984; Weidner 1936). Nevertheless, the assumption that caterpillars with irritative hairs will also be distasteful for birds often proves wrong. Specialized birds like cuckoos may even prey on pine processionaries and *M. rubi* caterpillars (Pro Natura 2000).

Coloration and defence proved to be poor predictors for larval activity patterns in lappet moths. This not only applied for the three species investigated in this study, but also in other confamilial species (cf. Table 1). Life-history traits may be much more informative, because comparing the species reveals marked differences in life-history.

Daily food intake in *M. rubi* is restricted to a small temporal window and caterpillars are therefore forced to compensate for this cost by a prolonged developmental time. This is possible because caterpillars are strictly univoltine, polyphagous, hibernant as full grown caterpillar, and may feed up to late autumn (Ebert 1994).

In contrast, *G. populifolia* is facultatively bivoltine and under laboratory conditions even polyvoltine. Fast development through frequent foraging may be the best strategy despite the risk of a reduced probability of survival in the field. Activity patterns of *G. populifolia* may therefore be influenced by a trade-off between being apparent during foraging to enhance development and being invisible during digestion to enhance survival. Furthermore, the thoracic eversible setae of *G. populifolia* may be used for defence in case of a bird's attack. Effectiveness of these setae as anti-predator defence has not yet been shown but seems likely as their morphology strongly resembles that of the confamilial species of the genus *Dendrolimus*, where these hairs were found to contain toxic substances (Kawamoto & Kumada 1984).

Life-history traits can also explain activity patterns in social caterpillars. Caterpillars of *E. lanestris* and *Malacosoma* spp. are strictly univoltine and develop very fast in early spring (Fitzgerald 1995; Ebert 1994). In contrast, caterpillars of an undetermined species of the genus *Gloveria* observed by Fitzgerald & Underwood (1998) feed on coniferous trees and have a long developmental time. Activity in this species is again restricted to nocturnal feeding although larvae are very hairy and aposematically coloured.

However, there is no consistent pattern of activity patterns and life history traits (cf. Table 1), indicating that several factors in combination influence feeding and resting behaviour of caterpillars and that generalizations are not appropriate.

Synchronicity of activity is a key factor for social species because it serves many purposes. Strongly synchronized foraging periods minimize conspicuousness to natural enemies. Furthermore synchronicity of all behaviours enhances thermoregulation (Ruf & Fiedler 2000; Casey *et al.* 1988), tent building (Fitzgerald & Willer 1983) and group defence displays (Costa & Pierce 1997).

It is obvious that the daily patterns of activity and rest exhibited by caterpillars under standardized conditions in the laboratory are unlikely to be fully realized under field conditions, where thermal constraints as well as encounters with predators and parasitoids may modify behaviour (Stamp & Bowers 1988). Nevertheless, only laboratory studies which exclude biotic and abiotic constraints on the caterpillars, give insights into genetically determined feeding patterns. Clearly, improved methods of continuously recording caterpillar activity patterns provide a convenient and powerful tool for gathering such knowledge which is crucial to understand the evolutionary ecology of caterpillar foraging more deeply.

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### References

- Balfour-Browne, F. 1933. The life history of the "smaller eggar moth", *Eriogaster lanestris* L.— Proc. Zool. Soc. Lond. **1933**: 161–180.
- Carlberg, U. 1980. Larval biology of *Eriogaster lanestris* (Lepidoptera, Lasiocampidae) in S. W. Finland.— Notul. Entomol. **60**: 65–72.
- Casey, T. M. 1976. Activity patterns, body temperature and thermal ecology in two desert caterpillars (Lepidoptera, Sphingidae).— Ecology **57**: 485–497.
- Casey, T. M., B. Joos, T. D. Fitzgerald, M. E. Yurlina & P. A. Young 1988. Synchronized foraging, thermoregulation, and growth of eastern tent caterpillars in relation to microclimate.— Physiol. Zool. **61**: 372–377.
- Church, S. C., T. D. Bennett, I. C. Cuthill, S. Hunt, N. S. Hart & J. C. Partridge 1998. Does lepidopteran larval crypsis extend into ultraviolet?— Naturwissenschaften **85**: 189–192.
- Comstock, J. A. 1957. Early stages of *Eutachyptera psidii* (Lasiocampidae), a rare moth from southern Arizona.— Lepid. News **11**: 99–102.
- Costa, J. T. & N. E. Pierce 1997. Social evolution in the Lepidoptera: ecological context and communication in larval societies. Pp. 402–442.— In: J. C. Choe & B. J. Crespi (eds.), The evolution of social behavior in insects and arachnids.— Cambridge University Press, Cambridge.
- Ebert, G. (ed.) 1994. Die Schmetterlinge Baden-Württembergs. Vol. 4, Nachtfalter II.— Eugen Ulmer, Stuttgart. 535 pp.
- Endler, J. A. 1978. A predator's view of animal color patterns.— Evol. Biol. **11**: 319–364.
- Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns.— Biol. J. Linn. Soc. **41**: 315–352.
- Fitzgerald, T. D. 1980. An analysis of daily foraging patterns of laboratory colonies of the eastern tent caterpillar, *Malacosoma americanum* (Lepidoptera: Lasiocampidae), recorded photoelectronically.— Can. Entomol. **112**: 731–738.
- Fitzgerald, T. D. 1995. The tent caterpillars.— Cornell University Press, New York. 303 pp.

- Fitzgerald, T. D., T. M. Casey & B. Joos 1988. Daily foraging schedule of field colonies of the eastern tent caterpillar *Malacosoma americanum*.— *Oecologia* **76**: 574–578.
- Fitzgerald, T. D. & S. C. Peterson 1988. Cooperative foraging and communication in caterpillars.— *BioScience* **38**: 20–25.
- Fitzgerald, T. D. & D. L. A. Underwood 1998. Communal foraging behavior and recruitment communication in *Gloveria* sp.— *J. Chem. Ecol.* **24**: 1381–1396.
- Fitzgerald, T. D. & D. E. Willer 1983. Tent-building behavior of the eastern tent caterpillar *Malacosoma americanum* (Lepidoptera: Lasiocampidae).— *J. Kans. Entomol. Soc.* **56**: 20–31.
- Gómez de Aizpúrua, C. 1988. Biología y morfología de las orugas. Lepidoptera, vol. VI.— Ministerio de agricultura pesca y alimentación, Madrid. 248 pp.
- Heinrich, B. 1979. Foraging strategies of caterpillars, leaf damage and possible predator avoidance strategies.— *Oecologia* **42**: 325–337.
- Heinrich, B. 1993. How avian predators constrain caterpillar foraging. Pp. 224–247.— *In*: N. E. Stamp & T. M. Casey (eds.), *Caterpillars – ecological and evolutionary constraints on foraging*.— Chapman & Hall, London.
- Heinrich, B. & S. L. Collins 1983. Caterpillar leaf damage, and the game of hide-and-seek with birds.— *Ecology* **64**: 592–602.
- Herrebut, W. M., P. J. Kuyten & L. de Ruiter 1963. Observations on colour patterns and behaviour of caterpillars feeding on Scots pine.— *Arch. Néerl. Zool.* **15**: 315–357.
- Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship.— *Oikos* **66**: 483–492.
- Kawamoto, F. & Kumada, N. 1984 Biology and venoms of Lepidoptera. Pp. 291–330.— *In*: A. T. Tu (ed.), *Insect poisons, allergens, and other invertebrate venoms. Handbook of Natural Toxins*, vol. **2**.— Marcel Dekker, New York.
- Kukal, O. 1993. Biotic and abiotic constraints on foraging of arctic caterpillars. Pp. 509–522.— *In*: N. E. Stamp & T. M. Casey (eds.), *Caterpillars – ecological and evolutionary constraints on foraging*.— Chapman & Hall, London.
- Lance, D. R., J. S. Elkinton & C. P. Schwalbe 1986. Two techniques for monitoring feeding of large larval Lepidoptera, with notes on feeding rhythms of late-instar gypsy moth (Lepidoptera, Lymantriidae).— *Ann. Entomol. Soc. Am.* **79**: 390–394.
- Nour, N., D. Currie, E. Matthysen, R. Van Damme & A. A. Dhont 1998. Effects of habitat fragmentation on provisioning rates, diet and breeding success in two species of tit (great tit and blue tit).— *Oecologia* **114**: 522–530.
- Pro Natura – Schweizerischer Bund für Naturschutz (ed.) 2000. Schmetterlinge und ihre Lebensräume. Arten, Gefährdung, Schutz. Band **3**.— Fotorotar AG, Egg. XI + 914 pp.
- Ruf, C. & K. Fiedler 2000. Thermal gains through collective metabolic heat production in social caterpillars of *Eriogaster lanestris*.— *Naturwissenschaften* **87**: 193–196.
- Seki, S.-I. & H. Takano 1998. Caterpillar abundance in the territory affects the breeding performance of great tit *Parus major minor*.— *Oecologia* **114**: 514–521.
- Stamp, N. E. & M. D. Bowers 1988. Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae).— *Oecologia* **75**: 619–624.
- Stamp, N. E. & Casey, T. M. (eds.) 1993. *Caterpillars – ecological and evolutionary constraints on foraging*.— Chapman & Hall, London, XIII + 587 pp.
- Stamp, N. E. & R. T. Wilkens 1993. On the cryptic side of life: being unapparent to enemies and consequences to foraging and growth of caterpillars. Pp. 283–330.— *In*: N. E. Stamp & T. M. Casey (eds.), *Caterpillars – ecological and evolutionary constraints on foraging*.— Chapman & Hall, London.
- Weidner, H. 1936. Beiträge zu einer Monographie der Raupen mit Gifthaaren.— *Z. angew. Ent.* **23**: 432–484.